

Shell microgrowth patterns of bivalves reflecting seasonal change of phytoplankton abundance

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Abstract. Seasonal patterns of shell microincrement growth in a venerid bivalve *Phacosoma japonicum* were analyzed for the three populations from Hakodate, Ariake, and Kagoshima Bays around the Japanese coasts. The northernmost Hakodate population in Hokkaido grew rapidly in a limited interval between late spring and summer. The number of microincrements within an annual increment in the specimens from this population was smallest (200-250 increments) among the three samples of populations examined, and each microincrement width was largest (0.25-0.3 mm) at the central part of an annual increment. By contrast, in the southernmost Kagoshima population in southern Kyushu, shell growth occurred slowly in a long term between early spring and fall. The specimens forming this population are characterized by having the narrowest microincrements (each 0.10-0.12 mm) and largest number of microincrements in the annual increment (300-350 increments). In this species, it has been confirmed that the growing season reflects the seasonal changes of phytoplankton abundance. The phytoplankton bloom usually occurs in spring in embayments of northern Japan and in summer in those of central and southern Japan. In Ariake Bay (central Kyushu), however, the phytoplankton becomes most abundant in winter and remains at low levels in the other seasons. The Ariake population of *P. japonicum* showed the most active growth in intervals between winter and early spring. In this sample, the microincrement width attained a maximum in the earlier portion of each annual increment, and the annual increment showed a particularly right-skewed pattern which reflects the winter phytoplankton bloom in this bay.

Key words : Bivalve, *Phacosoma japonicum*, Phytoplankton bloom, Shell microgrowth analysis

Introduction

Shell microgrowth analysis is a useful method for ecological research of extant and fossil molluscs, because microgrowth increments preserve information about environmental and physiologic conditions (Rhoads and Pannella, 1970; Kennish, 1980; Lutz and Roads, 1980; Jones, 1983). In the venerid bivalve *Phacosoma japonicum* treated in this paper, it has been confirmed that winter and spawning breaks are formed annually in the shell microgrowth pattern, and that they can be used to estimate the age of sexual maturity and shell growth rate in extant and fossil samples (Tanabe, 1988; Tanabe and Oba, 1988; Sato, 1994, 1995, 1996).

Growth and reproduction of bivalves are generally influenced by a number of environmental factors such as water temperature, salinity, and food availability. Sato (1998) suggested that monthly shell growth pattern and reproductive cycles of *P. japonicum* are strongly influenced by seasonal change of food availability, represented by phytoplankton abundance. Shell microgrowth analysis is useful to reconstruct the seasonal change of shell growth, so that it will be possible to estimate the seasonal change of phytoplankton abundance based on shell microgrowth analysis of fossil specimens.

In this study, to delineate the relationship between shell microincrement growth patterns and the seasonal change of phytoplankton abundance, seasonal patterns of shell microincrement growth in *P. japonicum* were analyzed for three populations around the Japanese coasts.

Material and methods

Seasonal changes of shell microincrement growth were examined for the samples from the subtidal sand flat of Kamiiso Coast, Hakodate Bay, southern Hokkaido (41°49'N, 140°42'E) and the intertidal sand flats of Nagahama Coast, Ariake Bay, central Kyushu (32°41'30"N, 130°33'30"E) and of Shigetomi Coast, Kagoshima Bay, southern Kyushu (31°42'30"N, 130°38'E) (Figure 1). Living individuals were collected monthly from Ariake and Kagoshima Bays during January-September, 1995, and those from Hakodate Bay were sampled on several occasions from September, 1991 to March, 1996 (Figure 1). Seasonal change of shell microgrowth patterns were analyzed for three-year-old specimens from each locality.

Shell microgrowth patterns were also examined for the samples from the other ten localities around the Japanese coasts (Figure 1). Of the ten samples, the two samples from

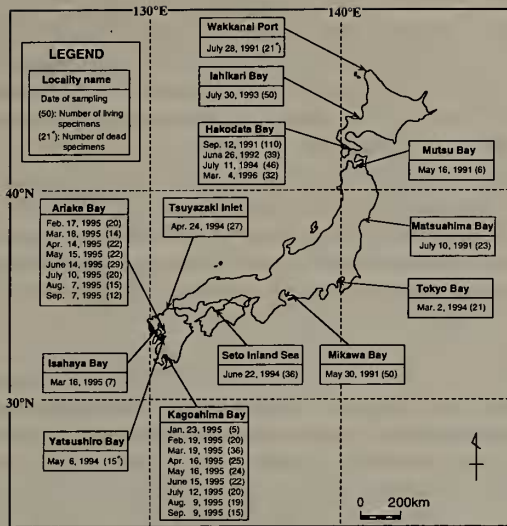


Figure 1. Locations and dates of collection for samples of *Phacosoma japonicum* treated in this paper. Number in parentheses shows the sample size.

Wakkanai Port and Yatsushiro Bay consist only of dead specimens, whereas those from the other eight localities are represented by living animals. Also, in Wakkanai Port and Ishikari and Hakodate Bays, animals from the subtidal zone were recovered from commercial port landings, and at the other localities, those from the intertidal zone were sampled manually at low tide.

To examine the shell microgrowth patterns, a single valve from each specimen was sectioned from the umbo to the ventral margin along the axis of maximum growth. The sectioned valve was polished and etched with 5% acetic acid for 10 minutes, and then an acetate peel was prepared for each specimen by pressing a sheet of acetyl cellulose film named as "Bioden R. F. A." (34 μm in thickness, Oken Shoji Co., Ltd.) on the etched surface flooded with acetone. Growth increments in each acetate peel were viewed by means of a Nikon V-16 profile projector at magnification, $\times 100$. The maximum width of each microincrement was measured successively from the umbo to the ventral margin using a digital micrometer (accuracy $\pm 1 \mu\text{m}$) attached to the profile projector.

Seasonal changes of shell growth and gonad development in the Hakodate, Ariake and Kagoshima samples were also

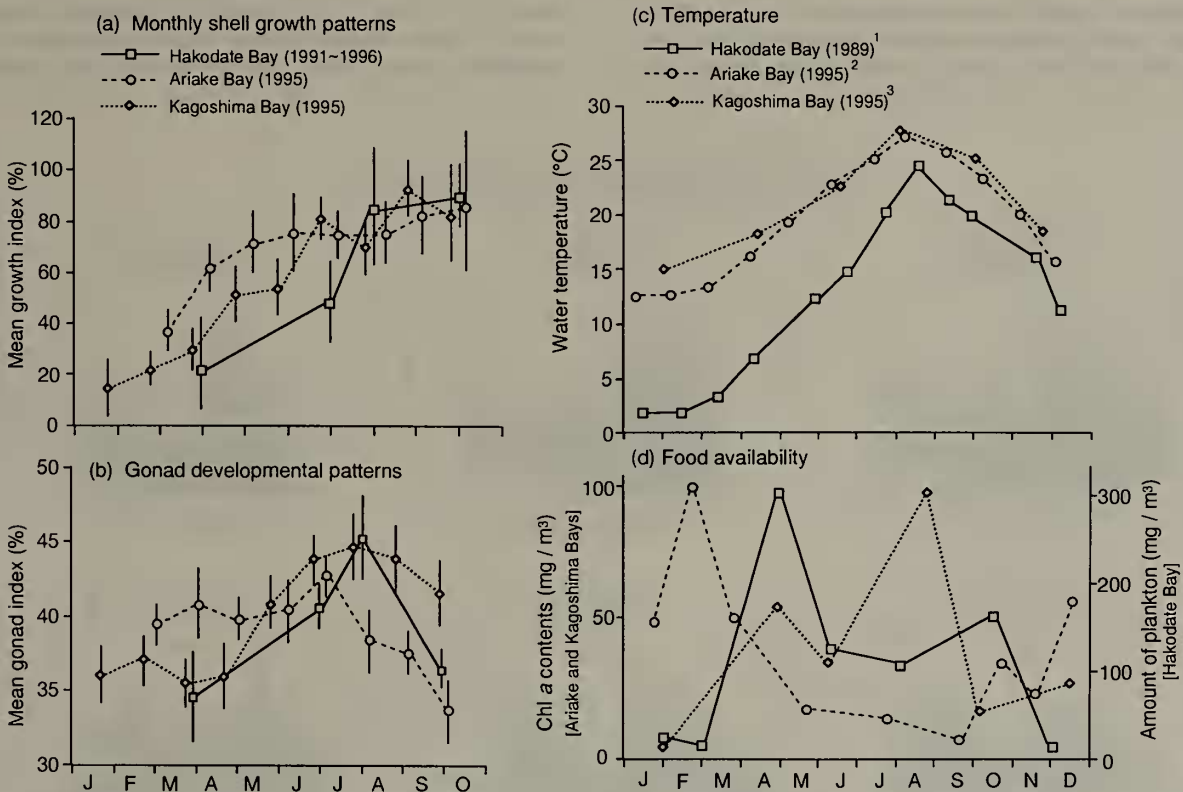


Figure 2. Seasonal changes of shell growth (a) and gonad development (b) in mature (>4 years old) specimens of *P. japonicum* from Hakodate, Ariake and Kagoshima Bays [mean value and the range of one standard deviation (vertical bar) are indicated], compared with annual variations of water temperature (c) and food availability (d) near the sampling localities. Sources of environmental data: (1) unpublished data of the Hokkaido Hakodate Fisheries Experimental Station in 1997, (2) unpublished data of the Kumamoto Prefectural Fisheries Research Station in 1997, (3) unpublished data of the Kagoshima Environmental Research and Service in 1997.

examined following the method described by Sato (1995, 1998). Gonad index [(gonad weight \times 100)/total soft body weight] and growth index [net growth (distance from last winter break to shell margin)/expected annual growth (distance from last winter break to expected next winter break)] were calculated in monthly collected samples. The extent of the expected annual growth for each individual was estimated using the Ford-Walford equation (Ford, 1933; Walford, 1946). The equation is expressed as

$$H_{R+1} = aH_R + b$$

where H_R is the shell height at the R th winter break (in mm), H_{R+1} is the shell height at the $R+1$ th winter break (in mm), and a and b are constants determined by a simple regression between H_R and H_{R+1} of different individuals of the same sample. Using this equation, shell height at the expected next winter break of each individual (H_{R+1}) can be estimated from shell height at the last winter break (H_R) and constants at each age class (a , b). Data of growth index and gonad index of the samples from Ariake and Kagoshima Bays were quoted from Sato (1998).

Results

Seasonal changes of growth and reproductive cycle in *P. japonicum* and some environmental factors

Figure 2 shows seasonal shell growth and gonad developmental patterns in the samples of *Phacosoma japonicum* from

Hakodate, Ariake and Kagoshima Bays and the seasonal changes of some environmental factors near the sampling localities. This species exhibits distinct geographic variation in seasonal patterns of shell growth and reproductive cycles (Figure 2a, b). Shell growth and gonad development were active from February to April in the population of Ariake Bay. For example, mean gonad index of the sample from Ariake Bay had already increased at a high value (more than 40%) as early as April, although the gonad index reaches a maximum in June (Figure 2b). On the contrary, shell growth and gonad development occurred during June and July in the Hakodate Bay population and from April to August in the Kagoshima Bay population. In these samples, mean gonad index kept to low values (less than 40%) during January to April and then increased rapidly in May and June (Figure 2b).

Because Ariake Bay and Kagoshima Bay are adjacent to each other, seasonal changes of water temperature and salinity are similar between them (Figure 2c; Sato, 1998). However, they are markedly different in the seasonal abundance of phytoplankton. In Kagoshima Bay, the amount of phytoplankton increases from June to August (Figure 2d). In Ariake Bay, however, phytoplankton abundance attains a maximum from January to March. The phytoplankton bloom generally occurs in spring in embayments of northern Japan and in summer in those of central and southern Japan (Iizumi *et al.*, 1990; Yamashita, 1982), so that the winter bloom in Ariake Bay is a very unique phenomenon in the Japanese coasts. Based on these data, Sato (1998) con-

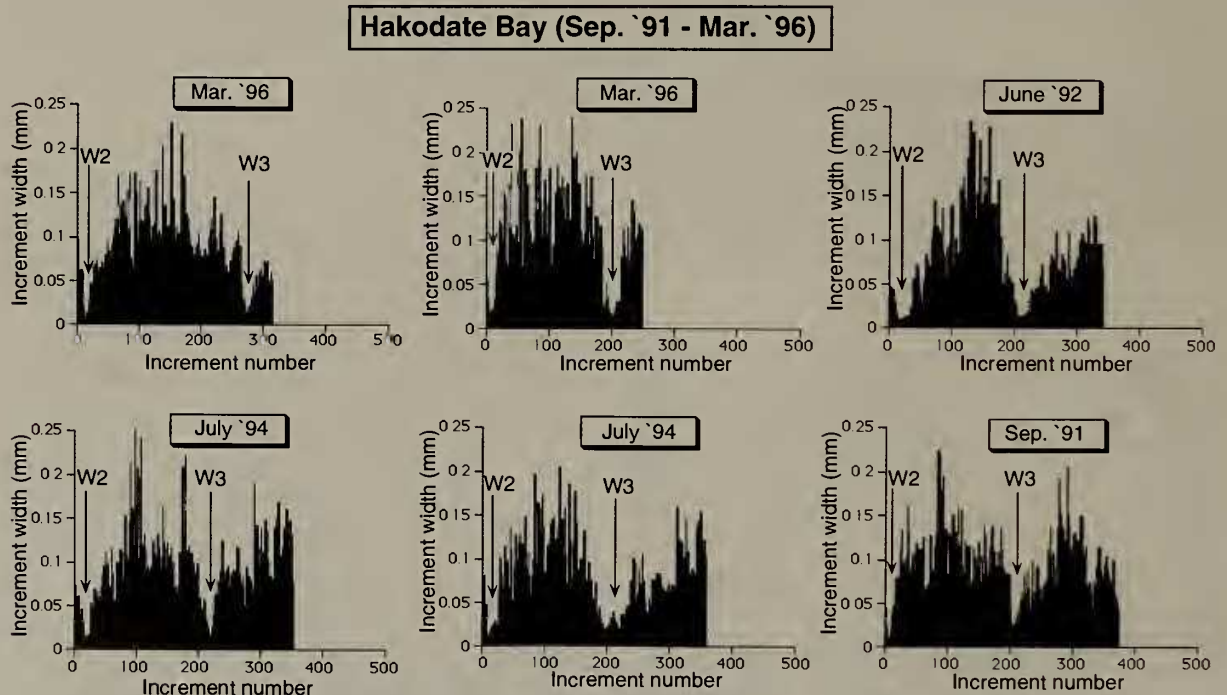


Figure 3. Shell microgrowth patterns from the 2nd winter break to shell margin in the six specimens of *P. japonicum*, each of which was collected from Hakodate Bay in March, 1996, June, 1992, July, 1994 and September, 1991 respectively. W2, W3: the 2nd and 3rd winter breaks which are fitted by eye, respectively.

cluded that growth and reproductive cycles of *P. japonicum* are primarily influenced by food availability not by water temperature.

Comparison of shell microgrowth patterns

Shell microgrowth patterns in the specimens from the three localities were examined and compared with each other. The specimens from each locality showed a similar growth pattern of microincrements. Shell microgrowth patterns in the selected three-year-old specimens from Hakodate, Ariake and Kagoshima Bays are shown in Figures 3 to 5.

The sample from Hakodate Bay

In the specimens from Hakodate Bay, a growth cessation mark represented by the discontinuity of the microincrement sequence is observed at the boundary between two annual increments (W2 and W3 in Figure 3). This cessation mark was caused by shell dissolution during the winter season (= winter break) (Tanabe, 1988), and in the specimens from this bay the winter break is clearer than in the other two bays. All of the specimens collected in March secreted fewer microincrements after the formation of the 3rd winter break than those collected in June and July. Each microincrement width rapidly increases in going from June to July and thereafter decreases in September. Thus it is suggested that the specimens in Hakodate Bay rapidly grow in a limited interval between late spring and summer, and in the other seasons they do not grow. Among the three samples

examined, the number of microincrements within the 3rd annual increment is smallest (200–250 increments), and each microincrement width is largest (0.25–0.3 mm) at the central part of an annual increment.

The sample from Ariake Bay

In the specimens recovered from Ariake Bay, microincrements near the end of an annual increment are narrow and crowded, so that the winter break is usually obscure (Figure 4). Because rapid shell growth occurs between winter and early spring in this bay (Figure 2a), winter breaks appear to be formed in late fall or early winter. Comparison of the shell microgrowth patterns among monthly collected specimens also reveals that after passing the 3rd winter break, microincrement width rapidly increases in February, and then gradually decreases from April to September (Figure 4). Because microincrement width attains a maximum in February, the microincrement sequence within each annual increment shows a right-skewed pattern. In this sample, each microincrement width is narrow (0.15–0.25 mm), and the number of microincrements is considerably large in the 3rd annual increment (250–300 increments) compared with the Hakodate sample.

The sample from Kagoshima Bay

In the specimens from Kagoshima Bay, the microincrement width increased slowly after passing the 3rd winter break, and microincremental growth continued during a long interval between March and September (Figure 5). There-

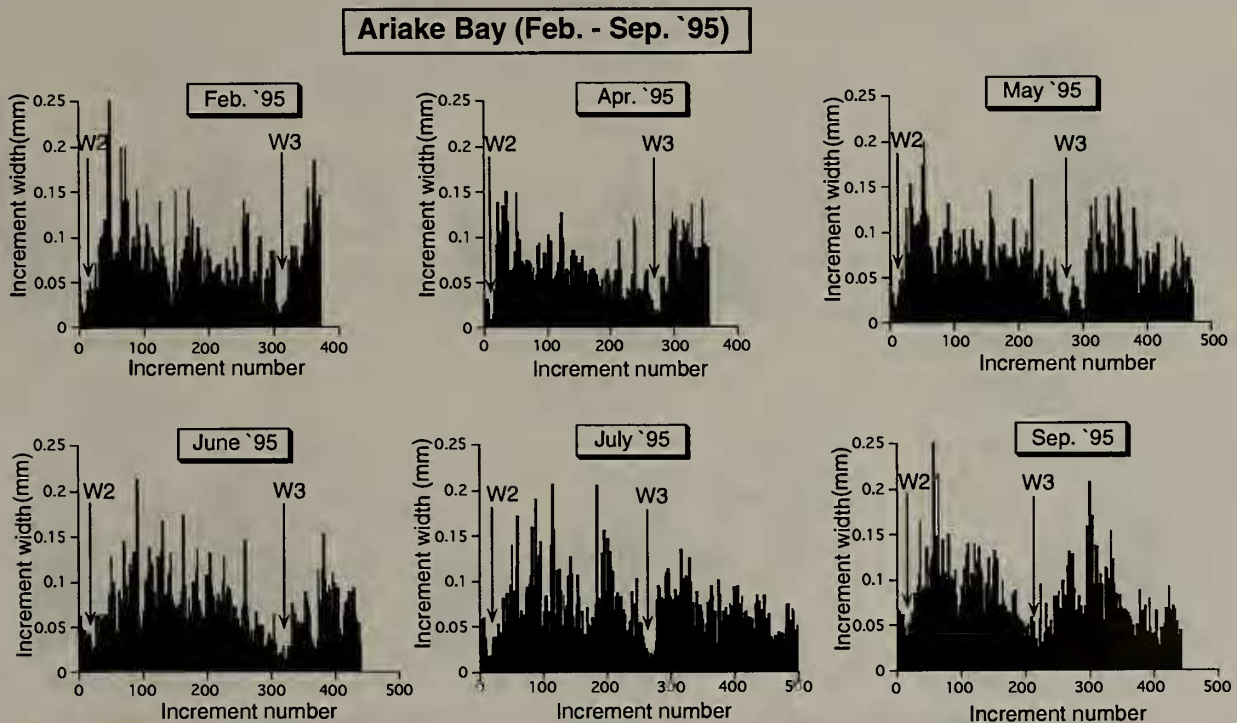


Figure 4. Shell microgrowth patterns from the 2nd winter break to shell margin in the six specimens of *P. japonicum*, each of which was collected from Ariake Bay in February, April, May, June, July and September, 1995 respectively. W2, W3: the 2nd and 3rd winter breaks which are fitted by eye, respectively.

fore, the maximum microincrement width is smallest (0.10–0.12 mm), and the number of microincrements in the 3rd annual increment is largest (300–350 increments) among the three samples examined. In this sample, the maximum microincrement width appeared during May and June, so that each annual increment exhibited a symmetrical pattern.

Also, a clear interruption of microincrement growth appears in the central part of the 3rd annual increment (S.B. in Figure 5). This interruption proved to be the result of a spawning event (= spawning break) (Sato, 1995). Based on this break, the onset of sexual maturity in this sample can therefore be determined as two years old.

Three types of shell microgrowth patterns and their geographical range around the Japanese coasts

Comparison of the accretionary pattern of microincrements among the thirteen local samples of *Phacosoma japonicum* revealed the presence of three types; i.e. northern, southern and Ariake types (Figure 6). These three types can be distinguished on the basis of the difference in the shape of the shell microgrowth pattern in the 3rd annual increment.

The northern type is represented by the sample from Hakodate Bay. The accretionary pattern of microincrements in the 3rd annual increment has a very sharp peak at the central portion, because every microincrement widens rapidly in a limited interval between late spring and summer.

Winter breaks are very clear because the ventral margin of each annual increment is partly dissolved in winter. Besides the Hakodate sample, the northern type includes all the samples from northern Japan; i.e. Wakkanai Port, Ishikari Bay (both in Hokkaido) and Mutsu Bay (northernmost Honshu). Ages of sexual maturity in those samples are at least four years, with maximum shell height of more than 6 cm (Table 1).

In the Ariake type typically represented by the sample from Ariake Bay, the accretionary pattern of microincrements in the 3rd annual increment is broad and right-skewed (Figure 6). Wide microincrements occurred during the limited interval between winter and early spring. Interestingly, this interval corresponds to the season of phytoplankton bloom occurrence (see Figure 2d). Specimens from Isahaya and Yatsushiro Bays also belong to this type. Age of sexual maturity of the Ariake-type specimens is four years, and maximum shell height of all samples in this type is more than 6 cm (Table 1).

The southern type is found in the specimens from Kagoshima Bay. The microincrement sequence in the 3rd annual increment is characterized by a symmetrical and low hillshape (Figure 6). Animals in Kagoshima Bay showed a remarkable growth in summer; the season of growth coincides with that of phytoplankton abundance. Therefore, the water temperature in growing season is much higher (20–30°C) than those of the other types (10–20°C). This kind of

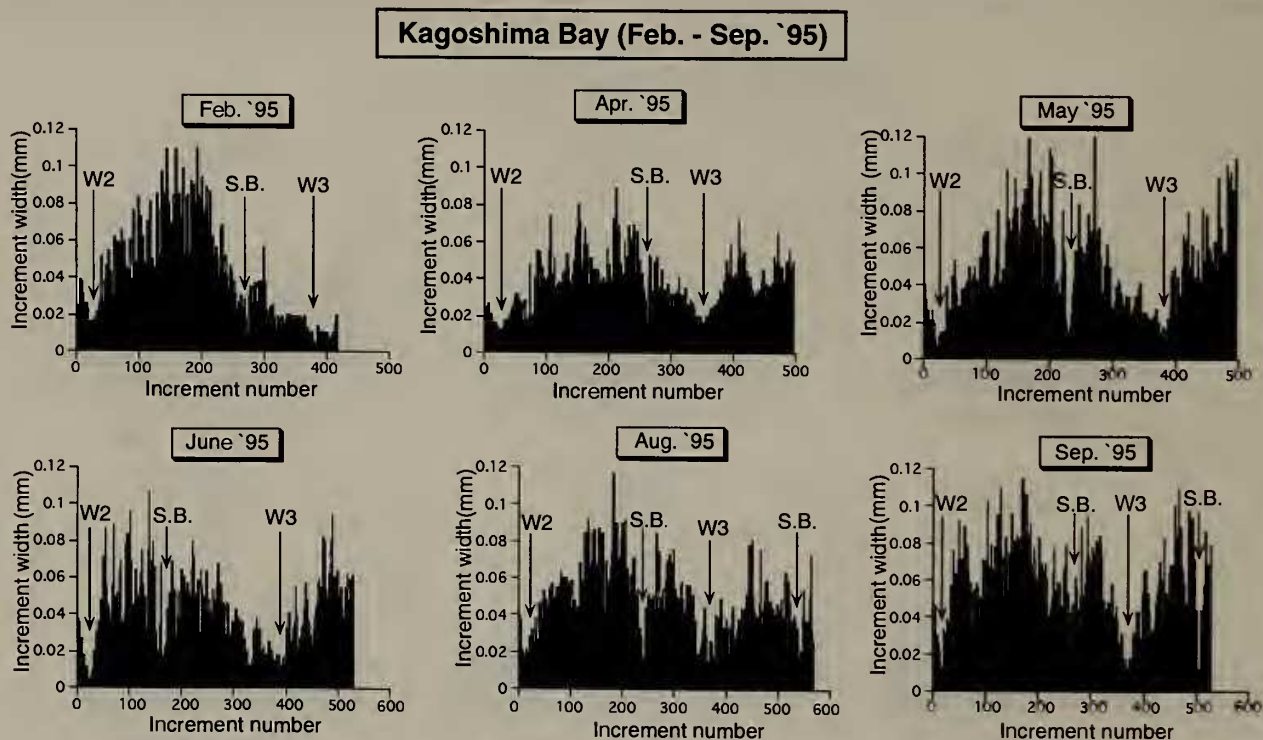


Figure 5. Shell microgrowth patterns from the 2nd winter break to shell margin in the six specimens of *P. japonicum*, each of which was collected from Kagoshima Bay in February, April, May, June, August and September, 1995 respectively. W2, W3, S.B.: the 2nd and 3rd winter breaks and spawning break which are fitted by eye, respectively.

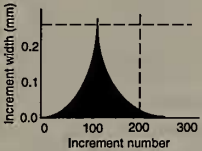
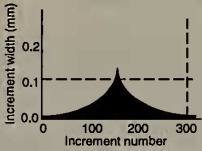
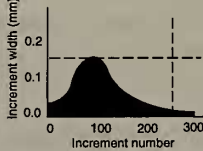
Types	Northern type	Southern type	Ariake type
localities of the populations	Wakkanai Port, Ishikari Bay, Hakodate Bay, Mutsu Bay	Matsushima Bay, Tokyo Bay, Mikawa Bay, Seto Inland Sea, Tsuyazaki Inlet, Kagoshima Bay	Ariake Bay, Isahaya Bay, Yatsushiro Bay
Maximum shell height	6.5 - 8.0 cm	4.6 - 5.8 cm	6.3 - 6.8 cm
Age of Sexual maturity	4 - 5 yrs	2 - 3 yrs	4 yrs
Growing season of this species	May - Aug.	Apr. - Sep.	Feb. - Apr.
Temperature in growing season	10 - 20 °C	20 - 30 °C	10 - 20 °C
Season of phytoplankton bloom occurs	Mar. - May	June - Aug.	Jan. - Feb.
Shape of shell microgrowth pattern in the 3rd annual increment			

Figure 6. Three shell microgrowth types recognized in the populations of *P. japonicum* around the Japanese coasts compared with the life history characteristics and environmental conditions of each type.

microincrement growth was widely recognized in the populations around the central to southern Japanese coasts including Matsushima Bay (northeastern Honshu), Tokyo and Mikawa Bays (both in central Honshu), Seto Inland Sea (Shikoku), Tsuyazaki Inlet and Kagoshima Bay (both in Kyushu). The geographical boundary between the populations showing northern-type and southern-type microincrement growth occurs between Mutsu Bay and Matsushima Bay (ca. 39°–40°N). Age of sexual maturity in the southern-

type populations is at most three years, and maximum shell height of all samples in this type is less than 6 cm (Table 1). Therefore, the southern-type populations can also be clearly distinguished from the populations of the other two types by the differences in life-history traits such as age of sexual maturity and maximum shell height.

Table 1. Summaries of life history and shell microgrowth patterns of *P. japonicum* at each locality. Maximum asymptotic shell height were calculated by Gompertz equation (see Sato, 1994).

Locality	Latitude	Maximum asymptotic shell height (cm)	Age of sexual maturity (yrs)	Number of micro-increments within the 3rd annual increment	Microincrement width of the largest increments (mm)	Shape of the 3rd annual increment	Type
Wakkanai Port	45° 25' N	8.02	> 5	150 - 200	0.25 - 0.30	Symmetrical	Northern type
Ishikari Bay	43° 10' N	7.21	5	200 - 250	0.25 - 0.30	Symmetrical	
Hakodate Bay	41° 49' N	6.49	4	200 - 250	0.25 - 0.30	Symmetrical	
Mutsu Bay	40° 52' N	6.63	?	200 - 250	0.25 - 0.30	Symmetrical	
Matsushima Bay	38° 22' N	5.15	3	250 - 300	0.10 - 0.15	Symmetrical	Southern type
Tokyo Bay	35° 19' N	5.80	3	200 - 300	0.15 - 0.20	Symmetrical	
Mikawa Bay	34° 46' N	5.21	3	250 - 300	0.10 - 0.15	Symmetrical	
Seto Inland Sea	33° 58' N	4.95	3	250 - 350	0.10 - 0.15	Symmetrical	
Tsuyazaki Inlet	33° 47' N	5.37	3	250 - 300	0.15 - 0.20	Symmetrical	
Isahaya Bay	32° 52' N	6.34	4	250 - 300	0.15 - 0.25	Right skewed	Ariake type
Ariake Bay	32° 41' N	6.53	4	250 - 300	0.15 - 0.25	Right skewed	
Yatsushiro Bay	32° 37' N	6.86	?	250 - 300	0.15 - 0.25	Right skewed	
Kagoshima Bay	31° 42' N	4.61	2	300 - 350	0.10 - 0.12	Symmetrical	southern type

Discussion

This study revealed that the populations of *Phacosoma japonicum* around the Japanese coasts can be classified into the northern, southern and Ariake types based on the shell microgrowth pattern (Figure 6). The boundary between the northern- and southern-type populations of this species corresponds to the northern limit of the zoogeographic ranges of typical Japanese temperate-water species such as *Meretrix lusoria*, *Macra veneriformis* and *Trapezium liratum* (Matsushima, 1984). Around the Japanese coasts facing the Pacific Ocean, these species do not live north of the Sanriku Coast (ca. 39°–40°N), where the water temperatures annually range from 8°C to 23°C (Tamura, 1966; Matsushima and Ohshima, 1974). *P. japonicum* is distributed in Mutsu Bay (ca. 40°N), but the shell microgrowth and life-history patterns in the northern-type populations markedly differ from those in the southern-type populations. These results suggest that the geographic boundary between 39°N and 40°N (annual range of water temperature from 8°C to 23°C) is a critical point reflected by the physiological conditions for many bivalve species living on the tidal flats.

The Ariake type included the samples from the three geographically neighboring bays in central Kyushu. Isahaya Bay is a small cove in Ariake Bay, so that seasonal change of phytoplankton abundance in this bay appears to be similar to that in the main part of Ariake Bay. In Yatsushiro Bay, phytoplankton bloom also occurred in winter (Tsuruta *et al.*, 1986). In summary, the growing season of *P. japonicum* is strongly influenced by the annual pattern of food (phytoplankton) abundance, and shell microgrowth patterns preserve well seasonal changes of phytoplankton abundance. Therefore, shell microgrowth analysis of fossil bivalves is expected to be useful in reconstructing seasonal change of phytoplankton abundance in paleoembayments.

Acknowledgments

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